XII. *On the Development of the Spores and Elaters of* Marchantia polymorpha.

By Arthur Henfrey, *Esq., F.R.S., F.L.S. &c.*

Read November 20, 1849.

M. MIRBEL*, in the first of his celebrated essays on the structure and development of *Marchantia polymorpha*, expresses himself in a note in the following terms:—"The origin of the elaters would, I think, be a curious discovery. I should not be astonished if most direct and positive observations led one day to the conclusion *that these organs are but one of the numerous modifications which the utricles undergo*. Such a result would decide many questions which we have long been endeavouring to solve."

In his second memoir on the same subject†, he announced the fact that he had observed the development of these bodies from the utricles; and the progress of vegetable anatomy since that time has made it a matter of certainty, that all the forms of the elementary tissues are to be referred to a cellular type. But so far as I can discover, all observers, who have hitherto investigated the development of the spores and elaters of the *Hepaticæ*, have overlooked certain important points. In the course of a series of observations on the development of spores, made in reference to the theories of cell-development in general, my attention was strongly attracted to a very peculiar condition which I met with in the young sporangia of *M. polymorpha*, and as I can find no notice of the phenomena in the works of previous authors, I am induced to publish an account of them.

The spores of *Marchantia* are produced, as is well known, in sporangia enclosed in peculiar receptacles or involucres situated at the base of the rays of the stellate body borne on the pedicel, on the under side. It is unnecessary to notice the characters presented by the envelopes of the sporangia, as these have long since been well described and figured; the whole course of development of these parts is beautifully illustrated in the memoirs of M. Mirbel already referred to.

The first indication of the production of the sporangia is the appearance of the organs called pistillidia, exactly resembling those of the other *Hepaticæ* and of the Mosses. Within the enlarged base of the pistillidium a small globule of a green colour is soon met with; this is the nascent sporangium, and in its subsequent development it enlarges within the expanding cavity of the pistillidium, acquiring a pyriform shape, and exhibiting at one period a little filamentous process at its apex. The nature or import of this process I cannot make out, but I found it also in *Sphærocarpus terrestris*, and it is

* Recherches anatom. et physiol. sur le *Marchantia*, &c., Mém. de l'Acad. Roy. des Sc. de l'Institut de France, vol. xiii. p. 337.

† Complém. des Observ. sur le *Marchantia*, &c. *loc. cit.* xiii. p. 375.

represented in the figures of most of the *Ricciaceæ* in Lindenberg's Monograph*. While the enlargement of the nascent sporangium tends to fill up the cavity of the pistillidium, the single layer of cells composing the wall of the latter is developed still more rapidly than the sporangium; its elongated neck disappears, and it is found in the nearly ripe fruit as a loose cellular envelope immediately enclosing the sporangium; when quite ripe it bursts above, exhibiting irregular teeth. The envelope of the globular sporangium of *Sphærocarpus terrestris* appears to me identical in its nature, but it remains green and does not burst: a little orifice in the apex, corresponding to the base of the neck-like portion of the pistillidium, may permit the escape of the spores; otherwise they can only become free by the decay of this involucre.

The walls of the sporangia of *Marchantia* are composed of a single layer of cells, at first almost cubical, and filled with chlorophyll-vesicles; but as they enlarge they become elongated in the vertical direction, the chlorophyll disappears, and spiral fibres, or more frequently annular bands, make their appearance upon the walls. These bands are of a flattened riband-like form, and of a yellow colour, the membrane of the walls of the perfect cells is hyaline, and the cavity contains only a few yellow granules. This structure of the wall of the sporangium of annular fibrous cells is analogous to that of the *Jungermanniæ* and to the spiral tissue of anthers, and is for a similar purpose, namely by its elasticity to cause the rupture of the mature parts as they become dried by evaporation.

No similar elastic tissue presents itself in the *Ricciaceæ*, in which moreover the elaters are absent†.

In all the foregoing points, my observations agree perfectly with those of M. Mirbel. Before proceeding to detail what I have seen in the development of the spores, it will be as well to give an account of what had been observed by preceding authors.

Mr. Griffith, in a note appended to M. Mirbel's first memoir‡, stated, with regard to *Targionia hypophylla*, that "in the young ovaries the elaters are not visible, and the seminules, united by a gelatinous substance, form as it were a continuous mass. They then seem to be vesicles filled with corpuscules, although when mature each is evidently a cellular body."

M. Mirbel§ remarks on the same plant:—"The nascent seminules are contained in the cells of a tissue which fills the young ovary; each cell contains three or four seminules. As the ovary advances in age, its internal tissue becomes dislocated, and is broken up into as many distinct utricles as there were cells, so that the little groups of seminules each have a utricle for an envelope.

"The seminules, young or old, are themselves simple utricles, which contain colourless spherules attached to their walls. This observation does not agree with the opinions of Mr. Griffith; according to him, the mature seminules are formed of cellular tissue.

"The elaters do not display themselves until some time after the dislocation of the tissue. They are slender, colourless, perfectly closed tubes, always with blind terminations (*en*

* Lindenberg, Monographie der Riccien, Nov. Act. Acad. Nat. Cur. xviii.

† According to M. Mirbel, the cellular tissue of the sporangium of *Targionia* (which has elaters) is not annulated, but the cells have half-rings on the internal and lateral walls, like the *Jungermanniæ*.

‡ *Loc. cit.* p. 371.

§ *Loc. cit.* p. 371–2.

cæcum), and often curved like a hook. At this epoch they contain colourless spherules which subsequently disappear.

"When the elaters are older they have acquired a yellow colour, and one would say that each served as a sheath to two long, very narrow bands, rolled concurrently and parallel, like a corkscrew, with very loose convolutions. There is an optical illusion here; the bands do really exist; but instead of being free in the interior of the tube, they are an integrant part of it."

In his second memoir*, M. Mirbel gives an account of the development of the elaters of *Marchantia polymorpha*:—"It (the sporangium) is at first merely a mass of tissue, composed of utricles filled with green spherules. But when the pistil had attained the degree of development last indicated, the internal utricles had become detached from one another, while those of the superficies remained closely united, and constituted a balloon-like sac, completely closed, in which the internal utricles were imprisoned. These were not all of one kind; some had been developed into long slender tubes, pointed at both ends, which most certainly still adhered by one of these ends to the internal surface of the sac; the others, in much larger numbers, polyhedral at first, had passed into a spherical form by the gradual rounding off of their angles. To each utricle elongated into a tube, a double series of utricles were feebly adherent. Both kinds were still filled with green spherules.

"As they advanced in age, the utricles composing the sac and those elongated into tubes underwent modifications, to which I must draw the attention of physiologists." [Three or four flattened rings, arranged parallel, appear on the walls of the cells of the sac; these become better defined, and at last acquire a yellow colour. My own observations on this point agree perfectly with those of M. Mirbel.] "The utricles elongated into tubes only differed from the others in form at first; they then possessed a delicate, simple, diaphanous, entire, uncoloured, membranous wall, but they soon became thickened, lost their transparency, and became marked all round, throughout their whole length, with two parallel streaks, closely approximated and describing helices. Then, increasing in size, their streaks became slits which cut the wall of each, from one end to the other, into two filaments, and the convolutions of these filaments separated, resembling the turns of a corkscrew. Finally, the two filaments acquired a rusty yellow colour, and the metamorphosis was so complete, that if I had not followed the modifications, step by step, I should now be afraid to say that these two filaments were at first one simple utricle; but the fact is constant, and I am convinced that whoever repeats the series of my observations, with the firm determination to let nothing escape which it is possible to see, will arrive at the same result as myself."

Bischoff gives no account of the development of the elaters, and evidently mistakes their origin, for he says†:—"Where we find among the spores, elaters *which, arising originally as elongated cells from the internal wall of the sporangium*, lie among the parent-cells of the spores, I should rather compare them to the cellular filaments which occur in the capsules of Mosses, *e. g.* in *Buxbaumia*, *Funaria*, &c., running across between the outer and inner membranes of the sporangium; and in *Polytrichum*, in part

* *Loc. cit.* p. 382. † Bemerkungen über die Lebermoose; Nova Acta Ac. Nat. Cur. xvii. p. 909 *et seq.*

between the latter and the columella; while in the *Hepaticæ* where the inner membrane is wanting, they run in free among the parent-cells of the spores."

Von Mohl* gives no account of the development of elaters; with regard to certain of his views on the development of the spores, I shall allude to the papers just cited, further on.

Gottsche† does not describe the development of the elaters, nor indeed the earlier conditions of the spores.

I now proceed to the results of my own researches on this subject.

The little green cellular body which is found within the pistillidium increases in size, and in the course of its growth its cells are differently modified; the external layers, over the whole surface, adhere together into a membrane, which becomes the spiral-celled membrane of the capsule; the cells contained within this layer produce the spores and elaters. I have not been able to determine satisfactorily the earliest conditions of the enclosed cells. In the youngest specimens I found it impossible to ascertain the true nature of the structure, on account of its delicacy, but I believe that Bischoff is certainly wrong in supposing the young capsule to be filled with a mucilaginous fluid (*brei*). Mr. Griffith and M. Mirbel state, that there exists a continuous tissue in *Targionia*; and Mr. Fitt‡ states that the apparently gelatinous contents of the capsule of *Sphærocarpus terrestris* exhibited a cellular appearance, when dried up, on the object-glass. From these facts and from analogy, I am inclined to believe that the young capsule is at first formed of a continuous cellular structure, and that the cells of this tissue become parent-cells, producing new cells within them, which they set free by becoming dissolved; exactly as occurs in the production of the parent-cells of the pollen-grains, in the continuous cellular tissue of anthers.

However this may be, it is certain that cells do become free in the cavity, producing the elaters and spores, and the condition and form in which they present themselves is very remarkable. M. Mirbel states that he found minute elongated cells, the young elaters, mingled with small squarish cells, the spores, which afterwards acquired a globular form. It is evident from this that he missed the earlier stages of the metamorphoses. I found the young capsules to contain elongated cells alone, and these of two sizes. The whole cavity of the capsule was filled up by elongated cells arranged side by side, and apparently radiating from the centre; a portion of these elongated cells were narrow, and were interposed between much longer and broader ones of the same form, in such a manner that scarcely any interspaces existed. The narrow cells are the young elaters, while the broader ones are the parent-cells of the spores. The subsequent development I have followed out clearly. The young elaters are elongated, slender tubes, attenuated toward each extremity; they are at first filled merely with an almost colourless, coagulable protoplasm. After a short time starch-granules make their appearance in them, the true

* Ueber die Entwickelung und den Bau der Sporen der Crypt-Gewächse, Flora 1833; Vermischte Schrift. 67. Ueber die Entwick. der Sporen von *Anthoceros lævis*, Linnæa 1839; Verm. Schrift. 84.

† Ueber *Haplomitrium Hookeri*, Nova Acta, vol. xx.. Ueber die Fructification der Jungermanniæ Geocalyceæ, Nova Acta, vol. xxi.

‡ London Journal of Botany, vol. vi.

nature of these bodies being readily determined by iodine. The starch-granules frequently lie within the young tube, in such a manner that they may easily be mistaken for the rudiments of the spiral fibres, but they are quite distinct from these, and disappear before the fibres begin to be deposited. I believe that the accounts given by some authors of the formation of spiral fibres in spiral vessels from rows of minute granules are incorrect, and have arisen from observation of starch-granules lying in rows, often running obliquely across the tubes. As the tubes grow they enlarge more in length than in diameter, and appear as very long, slender filaments; the starch-granules, and finally the protoplasm disappear, and faint streaks, denoting the nascent fibres, are at length to be perceived upon the walls. These gradually become more and more distinct, until in the mature elaters they present themselves as strong, flattened bands. In *Marchantia* there are two fibres, and the ends of these are confluent at the extremities of the tubes in which they are contained. More properly speaking, therefore, the fibre is one endless fibre twisted upon itself; the best possible condition of structure for the purpose. We may represent the condition of the fibres by a piece of string doubled, and with its ends tied together; this, when twisted up, unrolls immediately one end is set at liberty; or, if both ends are let loose at once, the whole piece springs away as it unrolls, just as the elaters of *Marchantia* spring out when the capsules burst. In unrolling the fibre it tears up the membrane of the wall of the tube, and when the elaters are examined after they have been discharged, the fibres are found somewhat unrolled, and the torn membrane is often no longer to be detected.

While the elaters are passing through these stages, the larger elongated cells exhibit a very remarkable series of changes, which appear to differ from everything that has yet been observed in analogous structures. They are at first filled, like the elaters, with a delicate, colourless protoplasm, in which float exceedingly minute granules; this substance is coagulated even by water, and still more strongly by alcohol, acids, and iodine. It is apparently the same substance that occurs in all young cells which increase by self-division. I have found it unmixed, as here, in young hairs, in the parent-cells of pollen before the formation of the septa, in the confervoid body which grows out from the embryonal vesicle of the *Orchidaceæ*, in the Yeast Fungus, &c. In most cells it very soon becomes mixed with starch and chlorophyll vesicles.

The elongated cells soon exhibit transverse streaks of a lighter colour, from the protoplasm separating into a number of portions, and cross membranes are produced at these places, dividing the tubular cells into a row of cells, all of square form, except the two end ones, which are attenuated toward the free point, and thus appear triangular in the side view. I could not make out whether the septa were formed by gradual growing in of the membrane; if so, the process must go on very quickly. Neither could I detect a double membrane; but this must exist, as the cells afterwards separate from each other at these points. Vertical septa often occur, producing a double row of cells from the original tube. M. Mirbel appears to have made his earliest observations subsequently to the breaking up of these rows of cells, and thus to have missed them. They are a constant phenomenon, and I know of no analogous structure, unless we compare them with the single rows of cells which first appear in the tissue of the anthers, and by subdivision become the parent-

cells of the pollen; but the cases are very dissimilar, since in *Marchantia* these rows of cells are produced from free tubular cells, in great numbers, after the dislocation of the tissue of the cavity of the sporangium.

About the time the cells separate from each other, the contents undergo a great change, which exactly resembles the change that occurs in the contents of the parent-cells and special-parent-cells of pollen when the formation of free cells is about to take place in their interior. The mucilaginous matter, or protoplasm, which was at first almost colourless, acquires a deep yellow colour, becomes much thicker, and exhibits a quantity of globular bodies which look like drops of oil. These globules are often described as granules, and some authors have mistaken them for drops of oil; others regard them as vesicles or vesicular cavities in the protoplasm; I believe them to be globular drops of the yellow protoplasm; they sometimes become confluent, but are not oil, since they acquire a brown colour, like the rest of the contents, with iodine, and are not dissolved by ether. They may acquire the appearance of vesicles by becoming coagulated on the surface, as this yellow protoplasm is readily coagulated even by water, but very strongly by alcohol or acids. The cells become filled with globules of this kind of all sizes, sometimes occupying half the cavity of the cell, but neither before nor after their formation did I meet with nuclei.

Soon after the cells become free, the yellow contents exhibit lighter streaks running across, which denote that they are separating into four portions; these are at length completely isolated and become coated by a proper membrane. They are the spores, and by the solution of the membrane of the parent-cells they become free. When free the contents become again clear and almost colourless, then the membrane becomes thickened and of a bright yellow colour, and the contents are changed into globules of pretty regular size which fill up the cavity. I never saw any trace of septa dividing the parent-cells into chambers, such as we meet with in the special-parent-cells of pollen. When the parent-cells in which the contents had parted into four portions were ruptured at one place, all the contents passed out and the membrane remained as a simple sac. When iodine was applied at the same stage, the portions were strongly coagulated, while the parent-cells expanded, but no trace of septa appeared.

Mohl states that the parent-cells of the spores of *Anthoceros lævis* are first divided into four chambers by septa, and that the same occurs in *Jungermannia epiphylla*, in the last of which the parent-cell divides into four separate cells, each containing a spore; which condition Mirbel asserts to be universal in the formation of spores. I could find no evidence of it; and Gottsche says, with regard to *Haplomitrium Hookeri*, that the empty parent-cells present marks which make them look as if they were chambered, but that all the spores pass out at one opening. It is quite possible that the enlarging spores cause the marks by their pressure against the enclosing membrane.

I could only distinguish a single coat to the ripe spore, and this grows out into a tube at one point in germination. The entire spore with its contents becomes colourless during this process, the yellow colour and the globules disappear, and after a short time chlorophyll-vesicles appear, which, when iodine is applied, are seen to be imbedded in a coagulable, colourless protoplasm. Mohl states that the spores of *Anthoceros* have two

coats, while Gottsche says that *Pellia* and *Blasia* have a single-coated spore, and *Fimbriaria* and *Preissia* apparently have two coats. I believe that this point can only be determined with certainty when the spores are germinating, and observation of this process leads me to the result that the membrane is simple in *Marchantia polymorpha*.

In conclusion, I cannot refrain from directing attention to the striking circumstance, that I met with no nuclei throughout the whole course of development. Mohl, in his essay on *Anthoceros lævis*, describes a series of phenomena connected with the appearance of nuclei, of which I saw nothing in *Marchantia*; neither did I see any nuclei during the development of the spores of *Sphærocarpus terrestris*, which I partially traced last spring. Sometimes the globular bodies in the yellow protoplasm present appearances which might be mistaken for nuclei, but careful investigation always led me to believe that these appearances were deceptive; and as I obtained clear and well-defined views of all the various stages, with fully sufficient magnifying powers to see nuclei if present, I am compelled to deny their existence here.

The main point, however, to which I wish to direct attention in this paper, is the singular manner in which the subdivisions of the cells take place, in order to produce the very dissimilar forms of long filiform elaters and spherical spores, from a tissue originally homogeneous.

London, Nov. 10th, 1849.

DESCRIPTION OF THE PLATE.

Tab. XI.

Fig. 1. A pistillidium containing the nascent sporangium at the bottom.

Fig. 2. More advanced sporangium *a*, enclosed in the membranous involucel, *b*, formed from the pistillidium. *c*. The outer involucre laid open.

Fig. 3. Portion of the wall of the sporangium 2 *a*, formed of cubical cells filled with chlorophyll.

Fig. 4. *a*. Two ripe capsules with their burst proper involucels, displayed by laying open the outer involucre; *b* and *c*. bursting sporangia.

Fig. 5. *a*. Portion of the elastic wall of the capsules 4, *b* and *c*. *b*. Two cells from the same, one with a spiral fibre, the other annular.

Fig. 6. Contents of the sporangium 2 *a*, consisting of broad and slender tubes.

Fig. 7. *a*. One of the broad tubes with the contents coagulated; *b*. one of the narow ones (elater).

Fig. 8. More advanced condition, with cross lines indicating the formation of septa: *a*. coagulated in water; *b*. by iodine.

Fig. 9. More advanced stage: *a*. fresh; *b*. with iodine.

Fig. 10. Later stage; the protoplasm becoming thickened in some cases. Vertical septa forming in some cells: *a*. in water; *b*. with iodine.

Fig. 11. Single and double rows of cells formed from the tubes, 7 *a*.

Fig. 12. *a*. Rows of parent-cells; *b*. young elater containing starch-granules; *c*. part of the same with iodine.

Fig. 13. Parent-cells in which the contents are beginning to produce the spores; the single one a free parent-cell in which the portions exhibit a membrane.

Fig. 14. Free parent-cells about to produce the spores.

Fig. 15. Parent-cells treated with iodine; the portions of contents coagulated and the membranes swelled; some cells burst and emitting contents. No trace of septa.

Fig. 16. *a*. Young spores become free, or adhering together in twos and fours, after the solution of the parent-cells; contents almost colourless; *b*. elater with the fibres appearing; *c*. portion of an elater more magnified to show the undefined appearance of the fibres.

Fig. 17. Ripe spores, bright yellow and filled with granules.

Fig. 18. Perfect elater.

Fig. 19. Portion of the same more enlarged.

Fig. 20. The end, to show the continuous condition of the fibre.

Fig. 21. Germinating spores: *a*. the membrane brownish, no contents visible; *b*, *b*, *b*. membranes hyaline, a few chlorophyll-vesicles formed; *c*. treated with iodine which colours the whole brown, and shows granular contents. The dark spots are the deep brown chlorophyll-vesicles.

The measurements are fractions of an inch.